PRESERVED LIGAMENTS IN AUSTRALIAN PERMIAN BIVALVES

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ABSTRACT. The Australian Permian 'burrowing' bivalves have large external ligaments which may be either replaced by calcite or have their outer surfaces preserved as external and internal moulds. Sections of two such replaced ligaments of *Pyramus laevis* and *Megadesmus nobilissimus* show three layers which probably correspond to the inner, outer, and fusion layers of living bivalves. The presence of fusion layer is to be expected from the lack of pallial attachment above the adductor muscles, and its presence in *Megadesmus* and *Pyramus* may prove to be useful in differentiating these shells from more or less homeomorphic living (and fossil) shells which have no fusion layer.

EXTERNAL ligaments of fossil bivalves may be preserved either as external moulds (Newell 1956, figs. 3*b*, 3*f*, 4*a*; Skwarko 1963, pl. 4, fig. 4; Runnegar 1965, pl. 15, fig. 15) or as silicified replicas (McAlester 1963, p. 6, fig. 65; Ciriacks 1963, pl. 4, fig. 9), and in either case are usually only visible on the outside of well preserved articulated shells. Exceptional specimens, such as the specimen of *Liebea squamosa* figured by Newell (1942, fig. 5, p. 29, pl. 15, fig. 3*b*), show details of the internal structure of the ligament which could only have been produced by selective solution or decomposition of different layers of the ligament; and Jefferies and Minton (1965, fig. 9) and Runnegar (1965, p. 234) have noted the preservation of ligamental structure in shells of Jurassic and Permian age.

Many of the desmodont bivalves of the eastern Australian Permian have large external ligaments which have been more or less completely converted to coarse granular calcite, and it has been possible to prepare transverse thin sections of the shell and ligament. The internal structure of the ligament has frequently been obliterated by recrystallization or replacement, but one specimen of *Pyramus laevis* (Sowerby) and one of *Megadesmus nobilissimus* (de Koninck) show layers which probably correspond to the original layers of the ligament.

The purpose of this paper is to describe the various layers of the ligament of the Permian bivalves and their method of attachment to the shell, and to suggest that the layers are similar in function and origin to those of many living shells such as *Tellina tenuis* and *Glauconome rugosa*.

SECRETION OF VALVE AND LIGAMENT

The following is a summary based on the work of Yonge (1948, 1953, 1957), Trueman (1949), Owen (1958, 1959*a*, *b*), and Owen, Trueman, and Yonge (1953).

The bivalved shell of lamellibranchs appears to have resulted from the lateral compression of a primitive uncoiled univalved shell about a median uncalcified strip, termed the ligament (Yonge 1953). Such an explanation is supported by the ontogeny of living bivalves whereby a single larval shell-gland secretes 'a saddle-shaped cuticular pellicle, which becomes calcified at two symmetrical points, right and left of the middle

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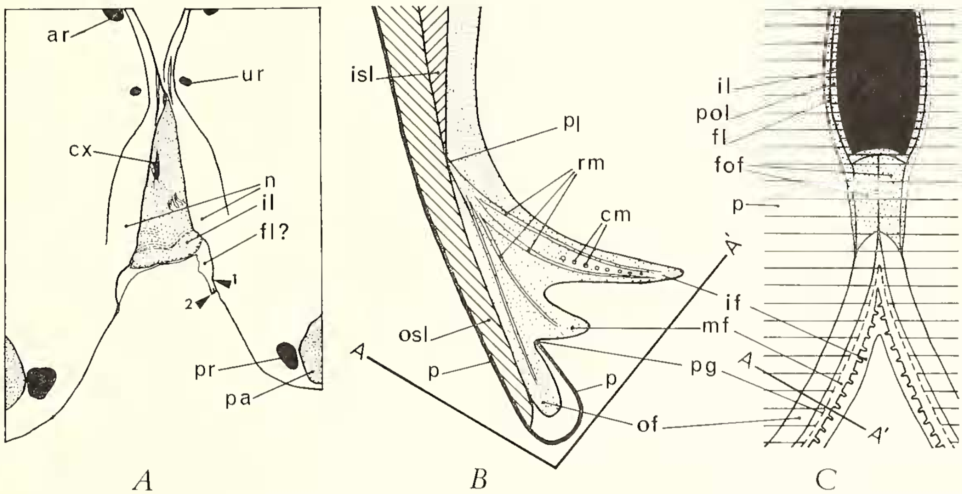
line' (Pelseneer 1906, p. 245). Thus the valves and ligament are parts of a single structure (the shell) and differ only in the degree of calcification of the protein matrix.

The shell is secreted by an envelope of tissue of comparable shape termed the mantle, and the neck of tissue which joins the right and left lobes of the mantle has been called the *mantle isthmus* (Owen, Trueman, and Yonge 1953). The mantle isthmus lies beneath and secretes the ligament, whereas the flanks of the mantle—the mantle lobes—secrete the valves.



TEXT-FIG. 1. A. Line drawing of the specimen of *Myonia valida* shown in Plate 19, figs. 1, 9 and Plate 20, fig. 10; ×1. Note the small piece of fusion (?) layer (2) which appears to extend beyond the posterior edge of the fossette (1).

B. Diagrammatic section of the margin of a bivalve shell and mantle corresponding approximately to the line *A–A'* in text-fig. 1C.

C. Diagrammatic external view of the posterior part of the ligament to show the relationship of the fusion layer to the secreting surfaces of the mantle.

ar, anterior retractor muscle scar; *cm*, circular muscles; *cx*, cracks in the inner layer of the ligament; *fl*, fusion layer; *fof*, fused outer surfaces of the outer mantle folds; *if*, inner fold of the mantle; *il*, inner layer of the ligament; *isl*, inner shell layer; *mf*, middle fold of the mantle; *n*, nymph; *of*, outer fold of the mantle; *osl*, outer shell layer; *p*, periostracum; *pa*, posterior adductor; *pg*, periostracal groove; *pl*, pallial line; *pol*, posterior outer layer of the ligament; *pr*, posterior pedal retractor muscle scar; *rm*, radial muscles; *ur*, umbonal retractor scar.

The valves and ligament are composed of two layers, the *inner* and *outer layers*, covered by a superficial but continuous *periostracum*. The inner layers of valves and ligament are secreted by cells comprising the external surface of the mantle and isthmus, whereas the outer layers and periostracum are formed only at the growing (peripheral) edge of the valve and ligament. (It is important to note that there is only one growing edge to the shell and that it is continuous from one valve to the other at the anterior and posterior ends of the ligament). Secretion of the periostracum takes place just inside the edge of the mantle in a structure termed the *periostracal groove* (*pg*, text-fig. 1 B–C) which lies between the outer edge of the mantle and the outer of two flaps of tissue that extend around the perimeter of the mantle. These two flaps together with the outer edge of the mantle, form the *mantle folds*, and are termed *outer*, *middle*, or *inner* according to their position relative to the outside of the shell (text-fig. 1 B–C).

The inner fold of the mantle contains radial (or orbicular) muscles which are attached to the shell along the pallial line as well as circumpallial muscles lying parallel to the mantle margin, and its function is partly protective and partly to control water flow into the mantle cavity. Cross-fusion of the left and right edges of this fold (with the development of appropriate pedal and siphonal orifices) may result in a firm muscular union of the ventral and posterior edges of the mantle lobes to produce siphons and a muscular 'floor' to the mantle cavity. The middle fold of the mantle edge usually bears tentacles and in some cases eye-spots, and its function is essentially sensory. The outer fold (the outermost edge of the mantle) is concerned solely with shell secretion; its outer surface gives rise to the outer shell layer, and, in the region of the mantle isthmus, the outer layer of the ligament, while the periostracum is secreted in the groove between its inner surface and the outer surface of the middle fold.

Most isomyarian bivalves have a more or less external ligament, most of which is situated behind the umbones. Consequently the mantle isthmus and ligament are asymmetric about a plane through the beaks at right angles to the hinge, and the major portion of accretionary growth of the ligament occurs at its larger (posterior) end. It follows that in unspecialized shells, posterior growth of the ligament is essentially like that of the valves, whereas decreased growth causes the anterior end to be somewhat modified. Furthermore, increasing specialization results in the partial or complete fusion of the left and right parts of the outer mantle fold at either or both ends of the ligament, so that the primitive or *primary* ligament (Owen *et al.* 1953) may be secondarily extended either by periostracum or by a new layer called fusion layer (Owen *et al.* 1953). The former is secreted if only the inner surfaces of the outer mantle fold are fused, whereas the latter is produced by the fused *outer* surface of this fold where it bends round from one valve to the other (text-fig. 1C).

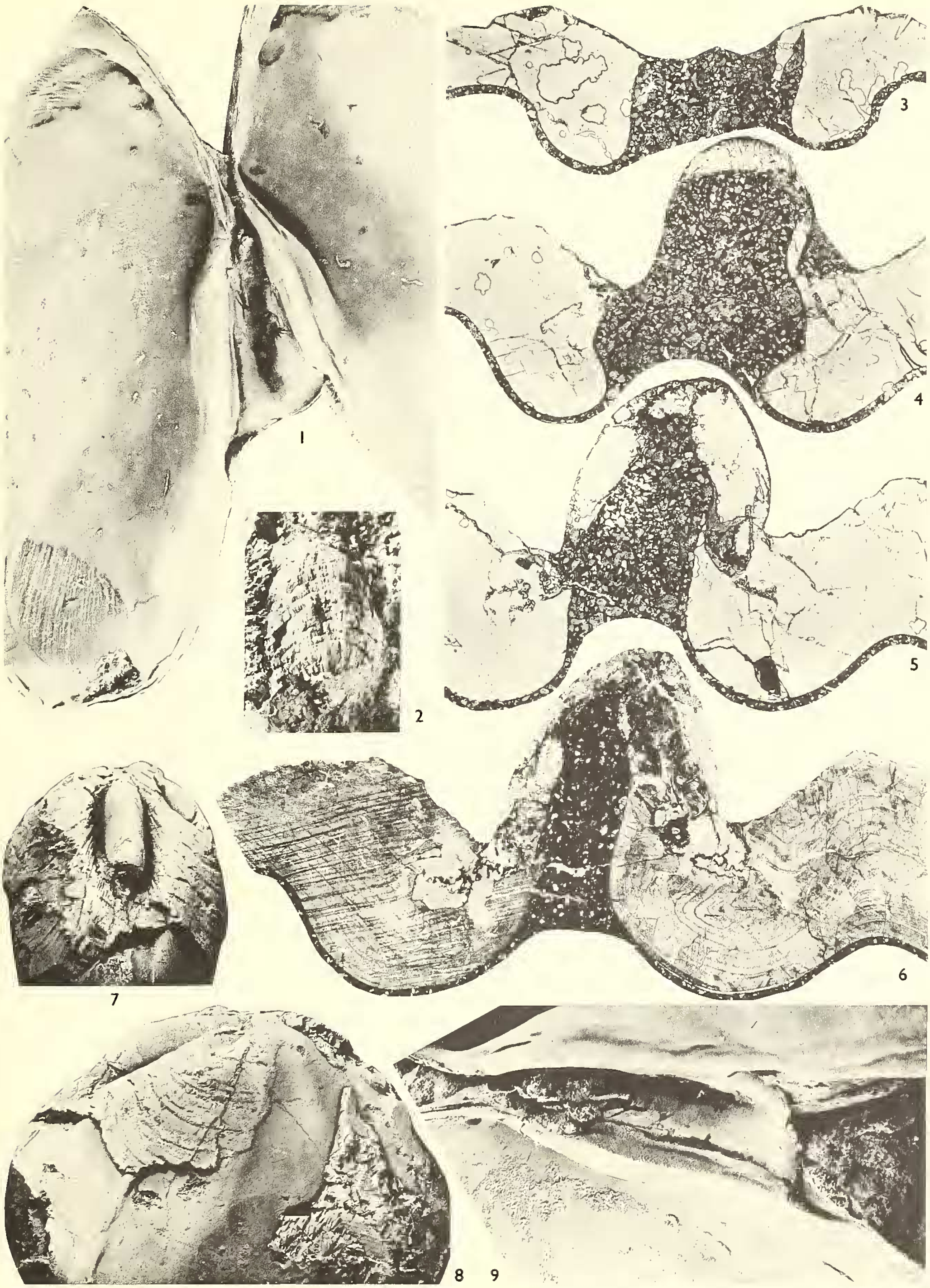
Megadesmus, *Pyramus*, and related members of the Pholadomyidae (Runnegar 1966) have an external C-spring-shaped ligament attached behind the umbos to a deep arcuate groove in each valve; the same type of ligament occurs in many unrelated living shells and has been described in detail from *Tellina tenuis* (Trueman 1942; 1949) and *Glauconome rugosa* (Owen 1959*a*). The following summary of the relationships of the various layers of the ligament of *G. rugosa* is taken from Owen (1959*a*, p. 63).

The interpretation of the structure of the ligament of *G. rugosa* will be more readily understood by comparing the sections shown in figures 4 and 5*a* to *i*, [*b* to *f* reproduced herein as *O* to *S* in text-fig. 3] with the diagrammatic representation of the ligament shown in figure 3 [herein text-fig. 2]. The posterior end of the primary ligament is secondarily extended by fusion layer (FL) and as a consequence,

EXPLANATION OF PLATE 19

Figs. 1, 9. *Myonia valida* Dana. 1, latex cast of internal mould of both valves and the ligament, viewed from the inside, ×¾. 9, the same specimen tilted to show the nymph of the right valve, ×1. See also text-fig. 1A. (AM F8206, Gerringong Volcanics, Wollongong, New South Wales.)

Figs. 2–8. *Pyramus laevis* (Sowerby), 1838. 2, partly decorticated ligament to show the fibrous structure of the inner layer, ×4. (AM F28113, Allandale Formation, Allandale, New South Wales.) 3–6, sections of the ligament of the specimen shown in figs. 7–8, ×5 approx.; compare with text-fig. 3*C–F*. 7–8, posterior and lateral views of partly decorticated shell with well preserved ligament, ×1. (AM F50457, same location as fig. 2.)



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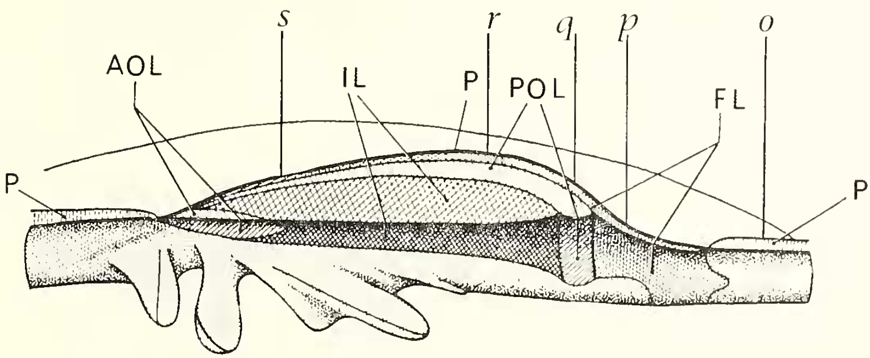
the functional ligament is composed of a superficial periostracum (P), fusion layer (FL) and outer (POL) and inner (IL) layers of the ligament. It extends posteriorly from the umbones approximately one-third the distance to the posterior end of the shell. Posterior to the primary ligament, the two valves are joined by an inverted U-shaped structure which is the fusion layer (FL) secreted by the fused outer surfaces of the outer folds of the mantle margins posterior to the mantle isthmus. In the mid-line between the two valves this fusion layer is secreted beneath the periostracum while laterally it extends beneath the calcareous layers of the valves. As growth proceeds the lateral regions of the fusion layer are progressively embedded in the calcareous layers of the shell and it undoubtedly serves to attach the ligament firmly to the valves. Outer layer of the ligament (POL) is secreted beneath the fusion layer by the outer marginal fold at the posterior end of the mantle isthmus where this bends round from one pallial lobe to the other, while the inner layer of the ligament (IL) is secreted by the epithelium of the mantle isthmus.

Underlying the inner layer at the anterior end of the ligament and extending a short distance anterior to the umbones is the anterior outer layer (AOL) secreted by the outer marginal fold at the anterior end of the mantle isthmus. Thus, all the possible constituents of the lamellibranch ligament (Yonge, 1957), with the exception of anterior fusion layer, are present and their relationship to one another particularly at the anterior end, are almost diagrammatically obvious.

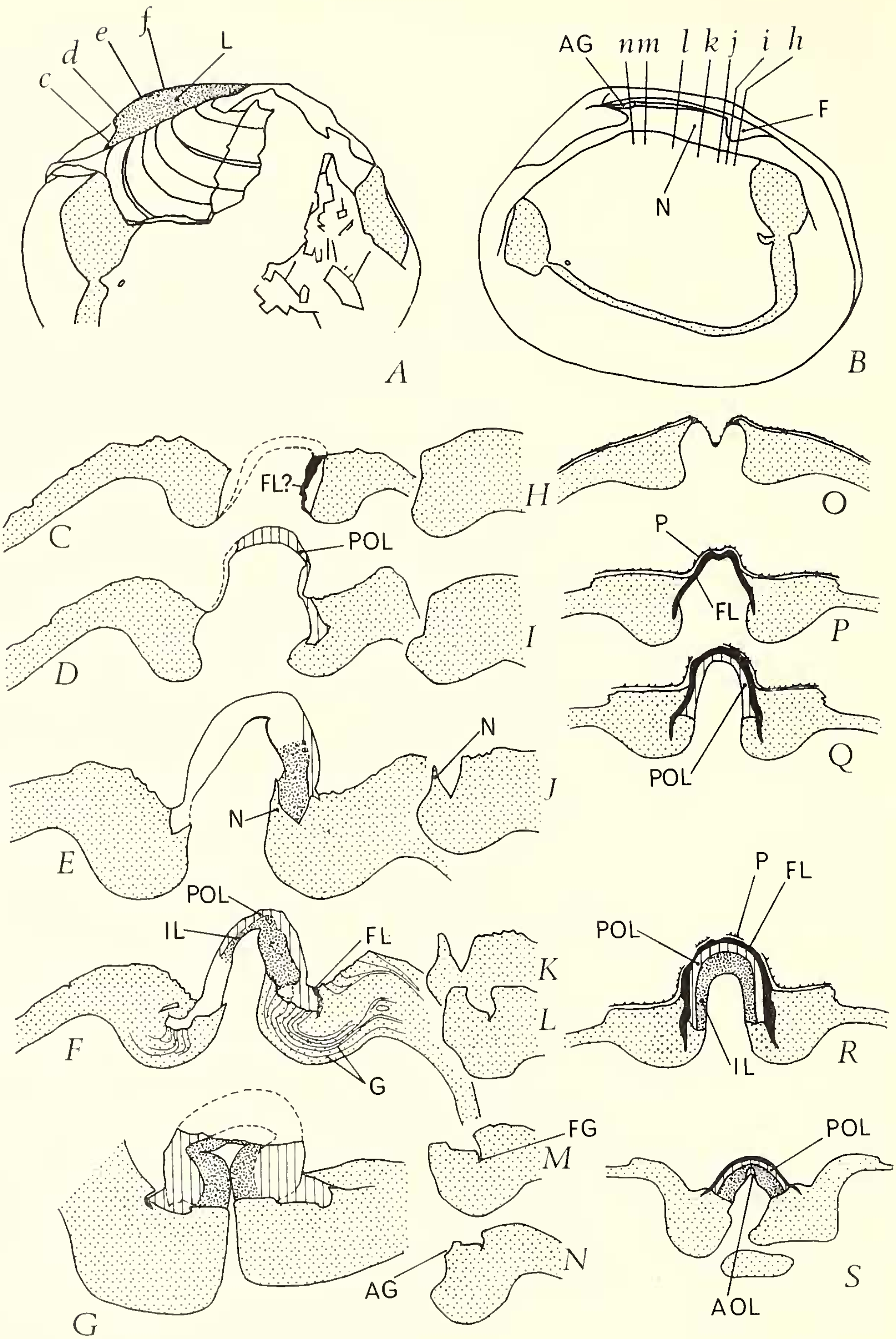


TEXT-FIG. 2. Semi-diagrammatic figure of the ligament of *Glauconome rugosa* cut longitudinally and viewed from the side (after Owen 1959*a*, fig. 3). AOL, anterior outer layer; FL, fusion layer, IL, inner layer; P, periostracum; POL, posterior outer layer. Sections cut at points *s–o* are shown in text-fig. 3*O–S*.

LIGAMENT STRUCTURE OF PERMIAN SHELLS

A detailed study of the ligament of the Permian bivalves has been possible because of two exceptionally well-preserved specimens of *Pyramus laevis* (Australian Museum F50457 and University of Queensland F47938), one of *Megadesmus nobilissimus* (UQ F45401), and one of *Myonia valida* (AM F8206). It seems likely that the ligament is fundamentally similar in related species and that the following description would apply in a general way to all of the Australian Permian members of the family Pholadomyidae (Runnegar 1966).

The ligament of *Pyramus laevis* is a short and robust structure situated externally behind the beaks (Pl. 19, figs. 7–8). Twenty-six acetate peels and one thin section were taken at significant intervals along the ligament of AM F50457, and several of these sections are reproduced in text-fig. 3*C–F* and Plate 19, figs. 3–6. However, since both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the shell and ligament are composed of crystalline calcite it was often difficult to interpret the somewhat crushed sections. Fortunately a completely undistorted and excellently preserved external mould of *Pyramus laevis* (UQ F47938, Pl. 20, figs. 7–9, text-fig. 3*B*) showing the ligament groove without the ligament was available. A rubber cast of this specimen was made and serial sections of the ligament groove were cut with a razor blade at intervals of about one millimetre. Camera lucida drawings of several of these sections are shown in text-fig. 3*H–N*. By comparing these sections with those of the shell plus the ligament it has been possible to suggest that at least three layers may have been present in the posterior part of the ligament of *Pyramus laevis*, and that these were probably inner layer (IL), posterior outer layer (POL), and fusion layer (FL). It is likely that an anterior outer layer and periostracum were present as well.

Attachment of the ligament to the shell. When the shell is viewed from above, the ligament groove is slightly arcuate and extends backwards from the beak (Runnegar 1965, Pl. 14, fig. 4). It is bordered on the inside by a strong vertical plate termed a *nymph* and the gap between the end of the nymph and the posterior (i.e. outside) edge of the ligament groove is the point where the secretory folds of the mantle edge bend round from one valve to the other. (Bernard 1895, p. 109) has called this gap the *fossette ligamentaire secondaire* or secondary ligamentary depression). Consequently, the inner layer of the ligament, which is secreted by the dorsal surface of the mantle isthmus, does not extend beyond the ends of the nymphs and is attached on either side to the upper edges of the nymphs (text-fig. 3*F*, *R*). By analogy with *Glauconome rugosa* (text-fig. 3*R*), the posterior outer layer appears to have been attached to the inner side of the V-shaped ligament groove (text-fig. 3*F*), and at the base of the groove is another narrower groove (FG) into which fusion layer was probably inserted (text-fig. 3*F*, *G*, *L–M*, compare with text-fig 3*R*, after Owen).

Bernard (1895) has pointed out that the *fossette secondaire* is merely the youngest section of the ligament groove, so that only the outermost layer of the ligament (in this case probably fusion layer) can extend backwards from the bottom of the fossette, since the posterior side of the fossette will eventually become the outer edge of the ligament groove. The posterior limit of the outer layer is therefore at or near the bottom of the fossette if fusion layer is present, and at the posterior end of the fossette if it is absent. However, fusion layer may extend for some distance beyond the ends of the primary ligament (Owen 1958), and, unlike the inner and outer layers, is not necessarily confined to the ligament groove.

Inner layer of the ligament. The boundary between inner and outer layers could be traced through 10 of the 27 sections of the ligament of *Pyramus laevis* and its position corresponds to that found by Owen in *Glauconome rugosa* and Trueman in *Tellina tenuis* (text-fig. 3). In living shells this layer is fibrous with the fibres perpendicular to the growing surfaces within the layer (Newell 1942, p. 28; Trueman, 1949). The fibrous structure of the layer in *Pyramus laevis* is well shown by the specimen figured in Plate 19, fig. 2,

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TEXT-FIG. 3. Sections of the shell and ligament of *Pyramus laevis* (*C–F*, *H–N*), *Megadesmus nobilissimus* (*G*, UQ F45401) and *Glauconome rugosa* (*O–S* after Owen 1959*a*, figs. 4*b–e*, 5*f*). The positions of the sections are shown in *A* (AM F50457, see also Pl. 19, figs. 1, 9), *B* (UQ F47938, Pl. 20, figs. 7–9), and text-fig. 2.

AG, anterior groove which probably contained AOL; AOL, anterior outer layer; F, *fossette ligamentaire secondaire*; FG, groove into which fusion layer was probably inserted; FL, fusion layer; G, growth-lines; IL, inner layer; L, ligament; N, nymph; P, periostracum; POL, posterior outer layer.

and the upper edge of the nymph of UQ F47938 shows the impression of fibres at right angles to the axis of the ligament (Pl. 20, fig. 8), thus providing additional evidence that the inner layer was attached to the upper edge of the nymph.

The inside surface of the inner layer is beautifully shown by a specimen of *Myonia valida* (Pl. 19, figs. 1, 9; text-fig. 1A) in which it extends backwards as far as the fossette and becomes very much thinner at its posterior end. The layer has several quite deep cracks in it (CX, text-fig. 1A) and the surfaces of these fractures also show the fibrous nature of the layer. Cracks of this type are common in the desiccated ligaments of shells removed from sea-water and they occur because of the low resistance this layer has to tensional stress.

Growth-lines within the layer are parallel to the inner surface of the ligament, so that the calcareous fibres are at all times perpendicular to the inner and outer surfaces of each growth lamella. Each growth lamella thickens posteriorly, and the younger lamellae overlap the earlier formed ones, so that the outer surface of the inner layer of the ligament is formed from the overlapped ends of the growth lamellae. This is well shown in the partly decorticated ligament of *P. laevis* (Pl. 19, fig. 2) in which the fibres at the posterior end of each lamella almost parallel the outer surface of the layer.

Outer layer of the ligament. The outer layer appears to be somewhat thinner than the inner and is probably composed of two parts—anterior and posterior outer layer. The latter covers the inner layer and probably extends beyond it as far as the base of the fossette. The gross structure of the posterior outer layer could be seen in transverse

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EXPLANATION OF PLATE 20

Figs. 1, 7–9, 13. *Pyramus laevis* (Sowerby). 1, plaster cast of lectotype of *Megadesmus cuneatus* (= *P. laevis*), $\times\frac{3}{4}$. (Brit. Mus. (Nat. Hist.) PL 682, Allandale Formation at Harper's Hill, near Lochinvar, New South Wales.) 7–9, dorsal and lateral views of latex cast of hinge to show the ligament groove nymph, and *fossette*. 7, $\times 1$; 8–9, $\times 2$. Note the fibrous nature of the upper surface of the nymph in fig. 8. (UQ F47938, 200 feet stratigraphically above the unconformity with pre-Permian strata at Durras South, south coast, New South Wales.) In fig. 7 the photograph of the hinge of F47938 has been superimposed on a photograph of another specimen (N.S.W. Geol. and Mining Mus. F7983, same location as fig. 1) to show the shell outline. 13, lateral view of latex cast showing part of the right valve and ligament, $\times\frac{3}{4}$. (UQ F47933, same location as figs. 8–9.)

Figs. 2, 6. *Megadesmus nobilissimus* (de Koninck). Lateral and dorsal views of left valve showing position of ligament groove. 2, $\times\frac{3}{4}$; 6, $\times 1$. (UQ F46635, Middle Gympie Formation, Chatsworth, north of Gympie, Queensland.)

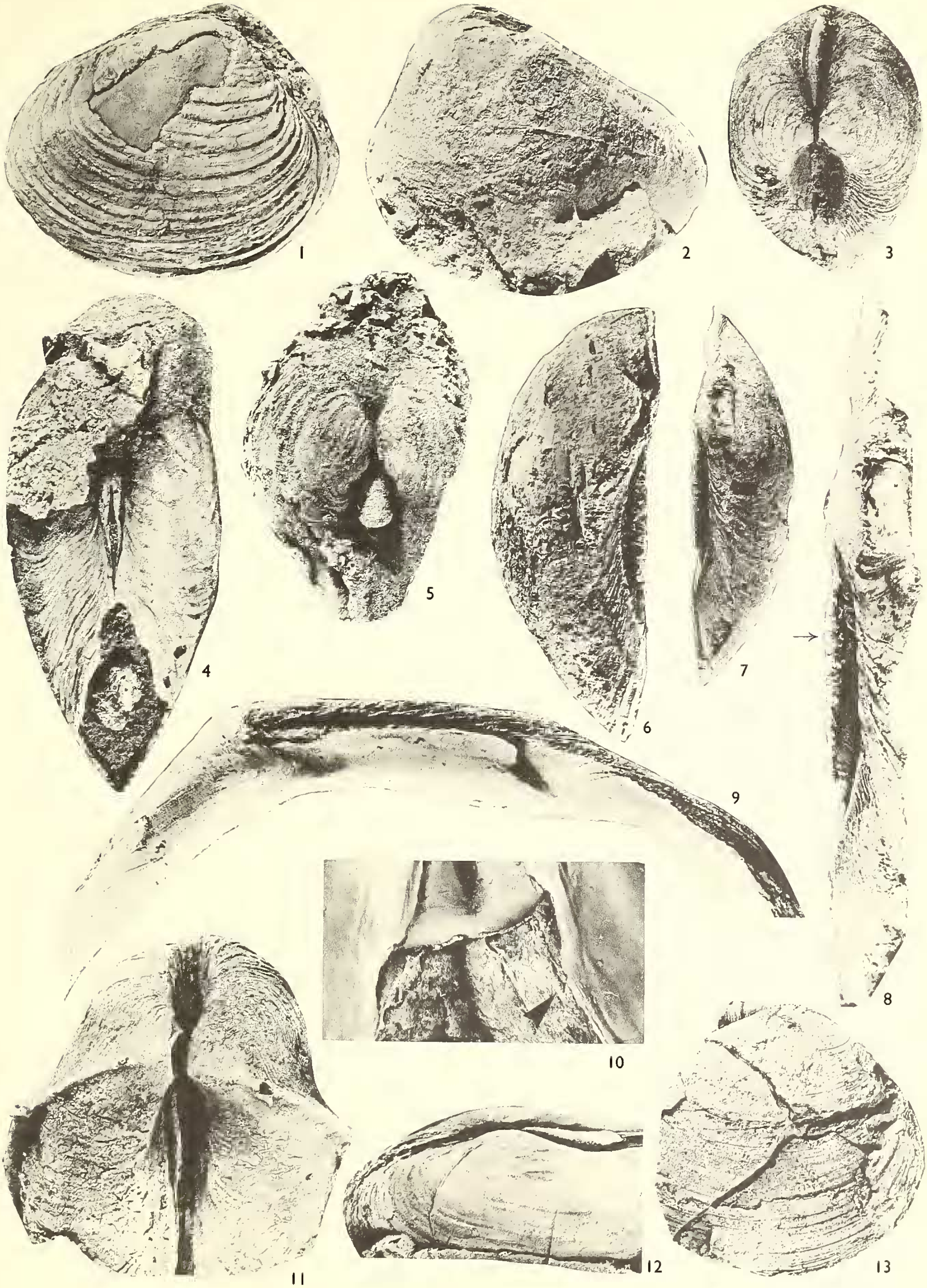
Fig. 3. *Astartila cytherea* Dana. Anterio-dorsal view of latex cast showing large external ligament. (AM F4735.)

Figs. 4, 5. *Vacunella curvata* (Morris). 4, dorsal view of both valves showing well-developed nymphs and long shallow fossette, $\times 1$. (AM F19201, Conjola Formation?, Bawley Point, Termeil, south coast, N.S.W.) 5, latex cast of external mould showing the ligament for comparison with fig. 4, $\times 1$. (Bur. Miner. Resour. Aust. CPC 7357, upper part of Middle Bowen Beds, Clermont area, Queensland.)

Fig. 10. *Myonia valida* Dana. Enlargement of posterior part of ligament of specimen shown in plate 19, figs. 1, 9, to show the maximum posterior extension of the fusion (?) layer (arrowed) beyond the end of the fossette, $\times 1$.

Fig. 11. *Myonia morrisi* (Etheridge). Latex cast of external mould showing ligament groove, $\times 1$. (UQ F21224, Homevale Beds, Homevale Homestead, northwest of Nebo, Queensland.)

Fig. 12. *Vacunella*? sp. nov. Latex cast of external mould showing ligament, $\times 1$. Bur. Miner. Resour. Aust. CPC 7358, Barfield Formation, Jerry Creek, 5 miles east of Baralaba, Queensland.)



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